

Selective Breeding in Fish and Conservation of Genetic Resources for Aquaculture

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Content

To satisfy increasing demands for fish as food, progress must occur towards greater aquaculture productivity whilst retaining the wild and farmed genetic resources that underpin global fish production. We review the main selection methods that have been developed for genetic improvement in aquaculture, and discuss their virtues and shortcomings. Examples of the application of mass, cohort, within family, and combined between-family and within-family selection are given. In addition, we review the manner in which fish genetic resources can be lost at the intra-specific, species and ecosystem levels and discuss options to best prevent this. We illustrate that fundamental principles of genetic management are common in the implementation of both selective breeding and conservation programmes, and should be emphasized in capacity development efforts. We highlight the value of applied genetics approaches for increasing aquaculture productivity and the conservation of fish genetic resources.

Introduction

Aquaculture is predicted to play a major and ever increasing role in meeting human needs for animal-source food. In terrestrial animal and plant species genetic improvement programmes have made a substantial contribution to agricultural productivity and viability. As a result of decades, if not centuries, of selective breeding and domestication in these terrestrial species, thousands of genetically distinct breeds, strains and varieties now exist worldwide and are collectively termed 'genetic resources'. By contrast, with the exception of a few fish species (see Gjedrem 2000, 2010; Ponzoni et al. 2011b), aquatic animals have undergone a limited amount of genetic improvement or domestication, and most aquaculture stocks in current use in developing countries are genetically similar or inferior to wild, undomesticated stocks (Brummett et al. 2004). This contrast raises two important differences between fish and terrestrial species in the context of conservation and use of genetic resources. Firstly, an enormous potential exists to improve aquaculture productivity through the application of selective breeding programmes and capitalize on the broad genetic diversity present in many wild fish populations. Secondly, because of the lack of well-defined domesticated breeds, the conservation of fish genetic resources is generally concerned with (i) the application of appropriate genetic management to ensure that cultured populations remain viable and productive, (ii) the possible impacts of cultured fish on wild populations and (iii) the preservation of habitats where (unique) wild populations reside. A range of methods of varying complexity is available for the selection purposes, but their suitability for different circumstances in aquaculture is not always clear. Similarly, there are several biological levels

at which the loss of a genetic resource is important, yet are not always considered when developing aquatic conservation initiatives or policies. In this review, we briefly present the main selection methods that have been used or advocated for aquaculture, and discuss their virtues and shortcomings. In addition, we review the manner in which fish genetic resources can be lost and discuss options to best prevent this. When possible, we make reference to practical examples of the application of both selective breeding and conservation approaches in aquatic animals. We also present evidence about the economic worth of genetic improvement programmes and discuss some of the challenges faced when implementing such programmes in aquatic animals.

Approaches to Genetic Improvement

Aquatic animals allow the implementation of several approaches to genetic improvement. These include hybridization and cross-breeding, chromosome manipulation, sex control, transgenesis and selective breeding. These are almost always mentioned in aquaculture genetics reports, papers and meetings without making a judgement about their relative practical value (e.g. FAO 2008). For instance, it is seldom, if ever, stated that of all the genetic approaches only selective breeding offers the opportunity of continued genetic gain, that the gains made can be permanent, that it is the only approach in which the gain can be transmitted from generation to generation and that gains in a nucleus can be multiplied and expressed in thousands or millions of individuals in the production sector (Ponzoni et al. 2007, 2008). In the cases they are useful, the other approaches result in 'once off' expressions of the benefit. They may be applied at the multiplication (hatchery) level, but not at the nucleus level.

Selection Approaches

General

We present the different selection approaches in increasing order of complexity, beginning with the simplest one. In each case, we refer to specific requirements that may constitute a limitation for their implementation in developing countries (a more detailed description of the methods is given by Ponzoni et al. (2006, 2009). Note that we assume that there is genetic variation for the trait(s) of interest in the population undergoing selection and that it does not suffer from problems (e.g. bottlenecks, inbreeding) created by earlier genetic mismanagement. Such problems could undermine the effectiveness of any selection programme (e.g. Smitherman

et al. 1988; Teichert-Coddington and Smitherman 1988; Huang and Liao 1990). The presentation could be considered repetitive and unnecessary in a livestock or crops context, but not in aquaculture where the application of quantitative genetics lags decades behind the two former fields.

Individual or mass selection

The terms 'individual selection' and 'mass selection' are often used interchangeably, and they refer to selection solely based on the individual's phenotype. It has been a common strategy with fish because of its simplicity. It does not require individual identification or the maintenance of pedigree records; hence, it may be considered the least costly method. In principle, it can produce rapid improvement if the heritability of the trait(s) under selection is high. Under those circumstances, however, there is risk of inbreeding because of inadvertent selection of progeny from few parents producing the best offspring, especially if progeny groups are large. For growth rate and morphological traits (easily assessed, expressed in both sexes), it can be suitable. By contrast, individual selection is not suitable for situations in which the estimation of breeding values requires slaughter of the animals (e.g. carcass and flesh quality traits) or challenge of some sort (e.g. selection for salinity tolerance or for disease resistance).

Hulata et al. (1986) carried out two generations of mass selection for growth rate with Nile Tilapia (*Oreochromis niloticus*) and observed no improvement over the original base population. They attributed the lack of response to selection to a number of possible factors, including inbreeding and genetic drift. They concluded that mass selection was not a promising method unless measures could be taken to control inbreeding. WorldFish (WorldFish Center, unpublished data) records indicate that the experience with Silver Barb (*Barbonymus gonionotus*) in Bangladesh and Thailand and Common Carp (*Cyprinus carpio*) in Vietnam has been of satisfactory response to the selection in early generations up to the fourth or fifth, declining sharply thereafter.

Overall, the evidence suggests that simple, unstructured, mass selection will result in problems unless the number of parents is large (Gjerde et al. 1996; Villanueva et al. 1996), and even so, chance could have a negative effect. Some form of structuring to control the parental contribution to the next generation appears necessary. If controlled pair matings can be carried out, the results of Bentsen and Olesen (2002) can be used to formulate the design of the breeding programme. They show that inbreeding rates can be kept as low as one per cent per generation if a minimum of 50 pairs are mated, and the number of progeny tested from each pair is standardized to 30–50 progeny. The guidelines provided by Bentsen and Olesen (2002) can be very valuable if they can be put into practice. However, we have found that in some developing countries, the conduct of a large number of pair matings, the subsequent containment of the full-sib groups and the sampling of a standard number of progeny to contribute to the next generation were tasks beyond the available resources, and we had

to change the strategy to that described in the following section.

Selection within cohorts and exchange of breeders

Eknath (1991) reports the genetic deterioration taking place in hatcheries in India owing to poor brood stock management. Among other measures to remedy, the situation he suggested that brood stock could be arbitrarily divided into several groups. Mating could then be performed between individuals from the different groups on a rotational basis to avoid inbreeding. In this section, we develop that notion further, based on the mating design used by McPhee et al. (2004) for weight selection in redclaw crayfish (*Cherax quadricarinatus*). These authors divided the population into cohorts, namely, groups sampled from a previously established foundation population. A selection line was created, consisting of 20 cohorts, where each cohort had 15 female and 10 male foundation parents. A control line of eight cohorts of the same size was also established. One hundred individuals were measured per cohort. Offspring of cohorts were hatched and grown in separate pens within a pond. At harvest time individuals of the heaviest weight in each cohort were chosen as parents of the next generation in the selection line, whereas individuals of average weight were chosen in the control line. In either case, selection was based on the difference between the harvest weight of an individual and its cohort mean. This within cohort selection aims to eliminate the environmental effect of cohorts on growth differences among individuals. The same number of individuals was selected from each cohort. Animals selected in one cohort were mated with those selected in another one to avoid mating related animals. After four generations of selection, harvest weight in the selection line was 1.25 times greater than in the control line.

By designing the selection programme in such a way that even in the case that only one pair from each cohort produced progeny, the inbreeding rate was not excessive, then we would be able to ensure that we would not run into problems because of inbreeding. With regard to the exchange of breeders between cohorts, this could be achieved by shifting the males born in one cohort to another one in a pattern as described by Nomura and Yonezawa (1996), following for instance Cockerham's cyclical mating system (Cockerham 1970). If we have information about the likely number of parents leaving offspring in a cohort (e.g. Fessehaye et al. 2006) then we can further refine the design. In practice, we have found that, in contrast to single pair matings, selection within cohorts with exchange of breeders between cohorts following a prescribed pattern is a feasible design even with limited resources. Field personnel feel comfortable with it, and will thus rigorously adhere to the instructions provided.

Within-family selection

The method requires identification of the families. This may be achieved by maintaining them in separate tanks, cages, hapas or any other means of containment, without necessarily tagging the fish. The criterion of

selection is the deviation of each individual from the mean of the family to which it belongs. Within-family selection is especially advantageous when there is a large component of environmental variance common to members of the same family. Full-sib groups reared in unreplicated hapas or any other form of containment fall into this category (e.g. see estimates in Ponzoni et al. 2005). Under such circumstances selection between families would be misleading from a genetic viewpoint because of the confounding between genetic merit and common environmental effects. If replacements are chosen so that every family contributes the same number of individuals to the next generation (e.g. choose one female and one male from each family) the effective population size is twice the actual (Falconer and Mackay 1996). However, not all the additive genetic variance is available for selection, but only a fraction equal to the coefficient of relationship among the family relatives in question (i.e. 0.5 and 0.25 for full and half sibs, respectively) will be available. The formula for the heritability of within-family deviations (h_w^2) is given by Falconer and Mackay (1996, p. 234). If for a particular trait the heritability in the population is 0.2 and the families are full-sib groups, then $h_w^2 = 0.11$. The lower within-family heritability can be compensated for by the high within-family selection intensity that can be applied without increasing the rate of inbreeding. The selection intensity within families will be limited only by the number of individuals tested per family. The number of families involved in the programme will determine the lower limit of inbreeding, which can easily be controlled by applying a rotational mating system such as that earlier suggested for selection within cohorts.

The use of within-family selection was recommended for SE Asian countries by Uraiwan and Doyle (1986). It was successfully applied in the selection programme that resulted in an improved Tilapia strain developed in the Philippines by the Freshwater Aquaculture Center (FAC) of Central Luzon State University. The selection programme and the strain's performance have been described by Abella et al. (1990), Bolivar et al. (1994), Bolivar and Newkirk (2000), Camacho et al. (2001) and Bolivar and Newkirk (2002). The selection line started from a base population combining four strains of Tilapia. Nineteen full-sib groups were established, and the basis of selection was body weight at 16 weeks of age. The heaviest male from a given family was mated to the two heaviest females of another family to avoid inbreeding. After 12 generations of selection, the genetic gain in body weight has been estimated at 12.4% per generation. The selection programme was conducted (from spawning to selection) in outdoor concrete tanks, but the strain also performed well in hapas and ponds. Camacho et al. (2001) comment that within-family selection was easy to manage and that taking care of inbreeding by means of a rotational mating posed no difficulties. The method reduces the need for tagging large numbers of individuals. They estimate that the implementation of a selection method that entailed the individual identification of large numbers of fish and a period of communal rearing would be more expensive and difficult to implement.

Combined selection

We use the term 'combined selection' in a broad sense, meaning selection that is based on individual information as well as on information coming from relatives (e.g. full and half sibs, progeny). In this case, all of the additive genetic variance is available for selection and the use of information from relatives increases the accuracy of the estimation of breeding values. Furthermore, relatives' records can be used to estimate breeding values for traits that require slaughter of the animals (i.e. carcass and flesh quality traits) or that entail a risky challenge (i.e. disease resistance, tolerance to some environmental component). This is not possible with the other methods (e.g. mass selection or within-family selection). Earlier work with fish (e.g. Eknath et al. 1998) used selection index theory to combine individual, full-sib and half-sib information. A selection index can be very useful in combining such information, but the approach has limitations that have been overcome with Best Linear Unbiased Prediction (BLUP) procedures (see Van Vleck 1993 for a detailed account). BLUP procedures rely on mixed model methodology for the estimation of individuals' genetic merit. In the case of aquaculture, all systematic effects (e.g. batch, sex, production environment, age variation) associated with traits of interest can be accounted for in the model fitted to the data. The maternal and common environmental effects because of separate rearing of full-sib families before tagging can also be separated effectively from the additive genetic variance. One particular advantage of BLUP procedures is that genetic gain can be estimated from the mean of the estimated breeding values in each year or generation of selection provided there are genetic links. There are now readily available computer programs (e.g. PEST, Groeneveld 1990; ASReml, Gilmour et al. 2002) that can estimate breeding values using full pedigree information. A drawback of BLUP selection is that if truncation selection on estimated breeding values is practiced, it also results in higher levels of inbreeding than individual selection, especially for lowly heritable traits. This is because BLUP uses family information, leading to co-selection of relatives. Hence, a mating strategy should be used that results in genetic gain while controlling the rate of inbreeding (e.g. Ponzoni et al. 2010).

Three documented examples of the successful application of combined selection to the improvement of fish in developing countries will be cited here (in all cases growth rate was the main focus of selection): (i) the GIFT project in Philippines, which reported genetic gains of 12–17% per generation in Nile Tilapia, over five generations (Eknath et al. 1998); (ii) the Jayanti Rohu (*Labeo rohita*) selective breeding project in India, which reported a genetic gain of 17% per generation over five generations (Reddy et al. 1999; Mahapatra, 2005, personal communication); and (iii) the selection project of a Malawian indigenous Tilapia, *Oreochromis shiranus*, where the accumulated gain over two generations was 13% (Maluwa and Gjerde 2007). GIFT and Jayanti Rohu have been tested extensively on farm and proven to outperform other strains used by farmers. We earlier mentioned that the GIFT and FaST strains have very

similar growth performance, but GIFT has shown greater survival rate, possibly due to the broader genetic basis in the population originally assembled and to the greater effective population size relative to FaST. Although the program with *O. shiranus* is at an earlier stage than the other two, the strain has now been tested extensively on farm with very positive results.

These three programs (GIFT, Jayanti Rohu, *O. shiranus*) have a number of features in common: (i) they all started with the assembly of a base population drawn from different sources to capture genetic variation; (ii) controlled matings of identified females to identified males were conducted and complete pedigrees were maintained; (iii) full-sib groups were kept together until tagging; (iv) approximately 50–200 fish per full-sib group were tagged and destined to communal rearing in a range of production environments to estimate genotype by environment interactions. In the case of GIFT and Jayanti Rohu, a selection index combining individual, full-sib and half-sib information was used to rank individuals on genetic merit, whereas BLUP breeding values were estimated in *O. shiranus*. BLUP procedures are also used in the selection of GIFT in the population that was transferred to Malaysia (Ponzoni et al. 2005). The sound design coupled with rigorous conduct and analysis accounts for the gains achieved in these programs. Furthermore, data sets of this nature, developed over a number of generations, provide great research opportunities in the area of estimation of phenotypic and genetic parameters, as well as of environmental effects and genotype by environment interactions. As a by-product of the genetic improvement programme, opportunities for local staff capacity building are created around it. Note that the amount of information that can be extracted from a pedigreed population is much greater than from a non-pedigreed one. This general model, packaged in what has been called 'GIFT Technology' has been advocated by the WorldFish Center for implementation in several developing countries (Thodesen and Ponzoni 2004).

Prospects for Genetic Improvement Programmes

Starting with a population with ample genetic variation is a trademark of successful fish genetic improvement programmes. Although this in itself is not a sufficient condition for success, it is indeed a necessary condition. The failure of some attempts to achieve genetic improvement with aquatic animals may have been due more to weaknesses in the base population than to the selection method utilized. Irrespective of the method of choice, continued genetic improvement will hinge upon the adequate balance between high selection intensity and the maintenance of low inbreeding rate.

Whereas there is evidence of response to selection in traits such as growth rate, of obvious benefit to the farmers, monitoring unfavourable correlated responses is important. For instance, Olesen et al. (2011) discuss likely alterations in behaviour as a consequence of selecting for growth rate. Furthermore, Shehzad (2009) reports epicarditis and incidence of heart abnormalities in farmed Atlantic salmon as a correlated response in

the genetic improvement programme for that species in Norway. Higher growth hormone levels in faster growing fish have also been correlated with increased aggression in some fish (e.g. Jonsson et al. 1998), which may have environmental consequences in the event of farmed fish escape (discussed later). As the genetic improvement programmes unfold, we should be alert to correlated changes that may negate the benefit from gain in other traits.

From an economic viewpoint, investment appraisal studies indicate very favourable benefit-to-cost ratios for genetic improvement programmes for both Nile tilapia (Ponzoni et al. 2007) and common carp (Ponzoni et al. 2008). This was shown to be so even for situations in which there was genotype by environment interaction (Ponzoni et al. 2008) and a single program had to service more than one environment. It is reasonable to think that these results can be generalized to other, similar, aquatic animal species.

Limitations and constraints during the implementation of genetic improvement programmes in fish often occur, particularly in developing countries. Issues are commonly related to financial resources, and to a paucity of human capacity in this field. Other constraints include technical issues related to individual identification of fish but these can be overcome with a relatively small investment. Further detail on limitations and constraints for genetic improvement of fish in developing countries is discussed in Ponzoni et al. (2009), and Lind et al. (in press).

Issues for Fish Genetic Resource Conservation

In this section, we summarize issues of genetic resource conservation relevant to commercially significant species utilized (or having potential to be utilized) for aquaculture. We recognize that many other fish species are subject to conservation or population management strategies, such as for managed capture fisheries; however, for the purpose of this review, we will deal with those issues pertinent to the aquaculture sector. Recent accounts of the use and exchange of genetic resources in aquaculture can be found for carps (Jeney and Jian 2009), tilapia (Eknath and Hulata 2009), salmonids (Solar 2009), shrimps (Benzie 2009), catfish (Na-Nakorn and Brummett 2009; Nguyen 2009), molluscs (Guo 2009) and other emerging aquaculture species (Nguyen et al. 2009), which provide additional detail complementary to this review.

Biological diversity is commonly categorized into three hierarchical levels: intra-species genetic diversity, species diversity and ecosystem diversity. For the purpose of this review, we categorize issues and concepts regarding the conservation of aquatic genetic resources into two hierarchical levels, namely, the intra-species genetic and population level, and the species and ecosystem level. In this section, we discuss how fish genetic resources are affected within each level, giving examples from the literature where possible, and attempt to identify important issues and approaches that may benefit future conservation and management efforts.

Intra-species genetic and population level

Here we are concerned with the conservation or management of a genetic resource at the population level, more specifically, the maintenance of gene variants (alleles) within a population. Maintaining genetic variation is important in preserving a population possessing certain valued attribute(s). It is also of broader value because of its critical role in a population's ability to genetically adapt to future environmental conditions (Allendorf and Luikart 2007). In addition, it will be important when genetic improvement through selective breeding is anticipated.

Fish generally have a high reproductive rate. A single breeding pair is capable of producing hundreds or thousands of progeny in a single generation. The frequently observed practice of aquaculturists producing a large number of individuals from only a few breeders can influence the maintenance of allelic diversity, the rate of inbreeding and effective population size (N_e). In addition to the potentially detrimental effects of inbreeding, one of the most important consequences of this at a population level is the likely marked effect of genetic drift. This may result in a population having altered gene frequencies that differ from those in earlier generations. This will be accompanied by a loss of alleles at a rate that is inversely proportional to N_e (Allendorf 1986). This phenomenon has been demonstrated in aquaculture species, in both developed and developing countries (e.g. Norris et al. 1999; Evans et al. 2004; Frost et al. 2006; Lind et al. 2009). It highlights the vulnerability of aquaculture populations to rapid loss of genetic variation.

Because of limitations in facilities, as well as in financial and human resources, it is often difficult to maintain fish populations that satisfy the minimum N_e recommended to retain evolutionary potential (i.e. $N_e > 500$, Franklin and Frankham 1998). In practice, it is more common to observe managed fish populations having N_e in the range of 50–100 (e.g. Gallardo et al. 2004; Kause et al. 2005; Ponzoni et al. 2010). Although populations of this size are deemed satisfactory for genetic improvement programmes (Meuwissen 2007), it is doubtful that they would remain viable in the long term in the event of substantial changes in the environment where they live.

Maintaining pedigree records of cultured fish populations can be difficult, which makes effective genetic management challenging. If reliable individual identification is not possible, high importance must be placed on employing appropriate culture practices to properly manage and conserve a genetic resource. The commonly used practices of mass-spawning can have a large effect on genetic variation and the rate of inbreeding in aquaculture populations. Fessehaye et al. (2006) showed high variance in reproductive success of mass-spawned Nile tilapias, where only one-third of males sired 70% of offspring. Other studies have similarly shown that hatchery and fish farming practices can be inefficient at capturing the genetic variation present in parent brood stocks (Brown et al. 2005; Frost et al. 2006). Whereas practices such as mass-spawning can be highly effective for producing large amounts of progeny with

limited facilities, when maintaining genetic variation is a priority mass-spawning should only occur in the context of a structured rotational breeding strategy (e.g. Fessehaye et al. 2007).

The use of polymorphic molecular markers can be a useful tool for ascertaining parentage and monitoring the loss of genetic diversity in fish populations. Such tools can provide an estimate of N_e , allelic diversity and heterozygosity (Avisé 1994), and are currently used in several fish conservation programmes (Ferguson et al. 1995; Vrijenhoek 1998). It is, however, still uncertain how effective inferences made from only relatively few (5–20) molecular markers is at preserving populations of interest or diversity at the genome level. This is an area of research deserving further investigation.

In contrast with livestock and crops, there is limited documentation and characterization of breeds, strains and varieties of fish species used for aquaculture. Neira (2010) compiled a list of over 40 known aquaculture genetic improvement programmes in developing countries that satisfy the basic concept of a breeding programme and are run by trained professionals. Although most have been in operation for <10 years and may be yet to develop sufficient differentiation to be categorized as a unique genetic resource, it is a valuable first-step towards documenting domesticated genetic resources of aquatic animals. Note, however, that distinguishing characteristics of such aquaculture strains are not commonly verified through controlled, rigorous comparisons with other strains (Ponzoni et al. 2011a), which can make prioritizing conservation efforts based on traits of interest difficult.

Cryopreservation of fish gametes is a promising opportunity for the conservation of both wild and domesticated fish genetic resources at a genetic, population or species level (Cabrita et al. 2010). There are several examples of successful cryopreservation for key aquaculture species farmed in developing countries, such as for Common Carp (Linhart et al. 2000), African Catfish (Viveiros et al. 2000) and Nile tilapia (Khaw et al. 2008). Although there has been limited success obtaining viable fish ova or fertilized zygotes after cryopreservation, the use of cryopreserved sperm could be valuable for the conservation of important breeds or populations of fish and is an additional area warranting continued investigation.

Species and ecosystem level

In this section, we summarize major issues of fish genetic resource conservation caused by the interactions *among* populations or species, particularly those caused by the interaction between escaped cultured fish and wild fish populations. Although recognized as serious issues, we do not cover fish conservation issues caused by over-fishing or habitat degradation, which have been comprehensively summarized previously (Helfman 2007). Note, however, that without effective prevention of over-fishing or habitat degradation, the *in situ* conservation of wild fish genetic resources will likely be unsuccessful (FAO 2008).

The relative ease with which hybridization (cross-breeding) occurs between closely related fish species has several implications for the conservation of fish genetic resources. Unlike terrestrial farm animals, fish are very difficult, if not impossible, to recapture in the event of escape from culture facilities. Hybridization and genetic introgression between species are a significant cause of extinction in the wild (Rhymer and Simberloff 1996). The potential consequences of hybridization between escaped cultured fish and their wild relatives are therefore a recurrent concern (Svasand et al. 2007), and a potentially major threat to wild fish genetic resources. The potential impact of cultured fish interbreeding with wild fish populations of the same species also raises concerns because of the possibility that natural genetic diversity or population structure may be adversely affected (Waples and Do 1994; Svasand et al. 2007). Molecular genetic evidence that inter-specific hybridization between cultured and wild fish is already occurring at local scales has been demonstrated in multiple regions, including Africa (D'Amato et al. 2007) and South-east Asia (Senanan et al. 2004). Similarly, within-species studies based on molecular markers have documented significant changes in the genetic structure and allele frequencies of wild fish as a result of deliberately released hatchery-propagated fish used for re-stocking purposes (Araki and Schmid 2010). This provides evidence that accidental escapees can alter the genetic composition of wild populations. However, it is yet to be comprehensively demonstrated that this has had any long-term impacts on population viability, although there are indications of immediate adverse effects that are yet to be confirmed over extended time scales (e.g. McGinnity et al. 1997, 2003; reviewed by Araki and Schmid 2010).

Genetically improved and non-native species constitute a substantial component of aquaculture production, especially in the developing countries (Silva et al. 2009). The use of non-native species, in particular, can be a highly controversial issue in some regions (Gozlan 2008; but see Vitule et al. 2009). Despite well thought strategies to prevent fish escaping from aquaculture facilities through the improvements in structural (or other) confinements (e.g. Mair et al. 2007), it would seem highly likely that fish escape will eventually occur. In conjunction with adequate confinement approaches, it has been proposed that broader, ecosystem-based approaches towards minimizing the impact of aquaculture escapes, such as ecological risk analysis (ERA), should be considered and adopted if possible (World-Fish Center 2002, Kapuscinski et al. 2007; FAO 2008). Although the use of ERA has been advocated on multiple occasions for addressing risks associated with proposed fish introductions, it is critical that its shortcomings and limitations are properly understood to utilize this approach effectively (see Cox et al. 2005; Cox 2008). Extensive engagement with key stakeholders and government agencies is increasingly believed to be an essential component of a robust ERA (Burgman 2005) and is highly relevant to situations concerning fish genetic resources where, for instance, the importance of food security versus biodiversity is often vigorously debated.

Baseline data relevant to understanding the impact of cultured-wild fish interactions is limited for many commercially significant aquaculture species, particularly in developing countries. Enormous progress has been made in recent years in the documentation of freshwater fish biodiversity in Africa (Darwall et al. 2011). Although not specifically focused on fish genetic resources for aquaculture, such efforts are highly valuable resources in this context. Phenotypic or molecular characterization of fish genetic resources can also be an important step towards developing appropriate conservation or management strategies (Helfman 2007). There are many examples of molecular approaches being utilized to identify population structure and the distribution of genetic diversity in wild fish genetic resources. However, an important remaining challenge is how to appropriately incorporate such information into formal conservation programmes or for ecological risk management strategies.

Prospects for Fish Genetic Resource Conservation

The implementation of successful conservation programmes for fish genetic resources often require collective effort by multiple stakeholders. Pullin (2005) has recently proposed several options and approaches for the conservation of farmed fish genetic resources and highlights the conservation of wild fish genetic resources is essentially nature conservation, having little similarity or overlap with the conservation of terrestrial farm animal genetic resources. Technical guidelines and recommendations have recently been prepared by the FAO in response to an expert solicitation on the state of the world's aquatic genetic resources (Bartley et al. 2007); providing guidance on key issues of fish genetic resource management and conservation, including issues of risk assessment, cryo-based gene banking and genetic management of cultured populations (FAO 2008). Lind et al. (in press) have also provided insights regarding issues and priorities for the conservation and use of fish genetic resources specific to aquaculture development in Sub-Saharan Africa. Many of these principles and issues dealt with for Sub-Saharan Africa apply for other regions across the world.

Institutional and governmental support is essential for the sustainable regulation and management of fish genetic resources, especially for developing countries where regulatory frameworks are often lacking. This has been emphasized in global policy recommendations on fish genetic resources (Bartley et al. 2007). Policy recommendations such as this, as well as others mentioned previously, indicate that the prospects of fish genetic resource conservation in developing countries will strongly depend on the ability of national governments to adhere to the principles and guidelines outlined therein. This is likely to require continued efforts to develop and strengthen internal capacity on such issues.

Concluding Remarks

Genetically improved strains are essential to aquaculture development. The application of proven quantitative

genetic theory should continue for relevant species. There is an ample proof of the success such programmes can have. Greater emphasis is required in the areas of dissemination of the improved stock to farmers to ensure impact at the production level. However, consideration must be given to the potential impacts of fish escapees and the conservation of wild fish genetic resources. Genetic management is necessary for both genetic improvement and conservation of genetic variation in cultured fish populations and should be emphasized in future capacity development initiatives. The documentation on cultured and wild fish genetic

resources will become increasingly important for conservation strategies as new strains are developed and aquaculture production further expands.

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Conflicts of interest

None of the authors have any conflicts of interest to declare.

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